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THE WEBS OF NEWLY EMERGED *ULOBORUS DIVERSUS* AND OF A MALE *ULOBORUS* SP. (ARANEAE: ULOBORIDAE)

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ABSTRACT

The web construction behavior of newly emerged *Uloborus* is more complex than heretofore supposed; large numbers of very fine non-radial threads are produced even though the spider moves only in radial directions on the web. This type of web may be universal in recently emerged *Uloborus* spiderlings, and a very similar web is made by mature males of at least one *Uloborus* species.

RESUMEN

La construcción de la telaraña por *Uloborus* recien salidas de la bolsa de huevos es mas compleja de lo que se pensaba; muchos hilos muy finos son puestos en sentidos no-radiales aunque la araña se desplaza unicamente en un sentido radial. Este tipo de telaraña puede ser universal entre las ninfas recien salidas del género *Uloborus*. El macho maduro de por lo menos una especie de *Uloborus* también construye una telaraña similar.

INTRODUCTION

The webs of immature orb weavers seem usually to be built on the same general plan as those of the adults, although they sometimes lack specialized adult characters peculiar to the given genus or species (e.g. *Zygiella*–Mayer 1952, *Nephila*–Comstock 1940, Wiehle 1931, *Scoloderus*–Eberhard 1975). The genus *Uloborus* is an exception to this rule, as the webs of newly emerged spiderlings differ substantially from those of the adults.

Wiehle (1927) was the first to study the webs of newly emerged *Uloborus* (spiderlings newly emerged from the egg sac will be termed "second instar spiderlings" in this paper since they have already passed through a stage inside the sac; this follows the usage of Peck and Whitcomb, 1970). He saw that the webs of second instar *U. walckenaerius* and *U. geniculatus* lack sticky spirals, but have intact temporary spirals, a large number of fine radial threads, and a concentration of white silk at the hub. He associated the lack of sticky spiral with the spiderlings' lack of a functional cribellum. Later Peters (1953) found that the webs of second instar *U. vicinus* resembled those described by Wiehle. Szlep (1961), working with *U. plumipes* and *U. walckenaerius*, described for the first time

the web construction behavior of second instar spiderlings. She found that their behavior during the early stages of web construction was essentially identical to that of older spiders: frame threads, radii, hub threads, and temporary spirals were all laid in the same way similar threads were laid by older spiders. But the second instars, instead of laying a sticky spiral after completing the temporary spiral, returned to the hub and laid great numbers of "additional" or supplementary radii which were somewhat thinner than the original "ordinary" radii. Szlep also found that third instar spiders usually spun "normal" orb webs with a sticky spiral and without additional radii as soon as they moulted, but that occasionally they spun intermediate types of webs with additional radii, intact temporary spirals, and sticky spirals all included.

To the best of my knowledge there are no previous records of mature male uloborids building any type of orb web.

This paper describes the webs and building behavior of the second instar nymphs of a fifth *Uloborus* species, *U. diversus*. Some details not noticed in the webs of the other species are discussed, and a very similar web built by a mature male of *Uloborus* sp. is also described.

MATERIALS AND METHODS

Uloborus diversus spiderlings were raised from eggs laid in captivity, and were kept and observed under the conditions described by Eberhard (1972). Their webs were photographed both uncoated and coated with fine white powder (cornstarch) in the indirect lighting arrangement illustrated by Langer and Eberhard (1969). The webs of male *Uloborus* sp. were photographed in the field by coating them with cornstarch and using a portable flash (Eberhard, 1976). Specimens of these males, which cannot be identified to species at this time, are deposited in the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 02138, U.S.A., and are numbers 879, 890, 902, and 1015 of a collection of spiders whose webs have been photographed.

RESULTS

The webs of second instar *U. diversus* (Fig. 1) were essentially identical to those of *U. plumipes* and *U. walckenaerius* pictured in Szlep (1961). They differ from her description however in having large numbers of non-radial threads, most of which are more or less straight and parallel to their neighbors, and some of which extend beyond the frame threads. Similar non-radial threads are visible in Szlep's photos of *U. plumipes* webs. These threads are extremely thin and nearly invisible even when brightly illuminated.

As in other *Uloborus*, the behavior of second instar *U. diversus* spiderlings during the construction of the hub, radii, frame, and temporary spiral threads was similar to the construction behavior of older conspecifics (Eberhard, 1972) except that the loops of temporary spiral were closer together in relation to the size of the spider's body than those in older spiders' webs. The construction behavior involving the supplementary radii differed from the construction of the original radii in several ways however. Spiders made only one attachment rather than a series of attachments at the hub after laying each additional radius. They did not direct either leg I laterally after reaching the hub, but simply turned and held the radii (or the outer hub threads?) directly in front of them with both I's. They laid successive supplemental radii closer together; in one typical sequence, a spider laid supplemental radii toward the positions 6, 5, 5, 3, 2, 1, 11, 11, 10, 10, 11, 11, 12, 9, 10, and 9 o'clock.

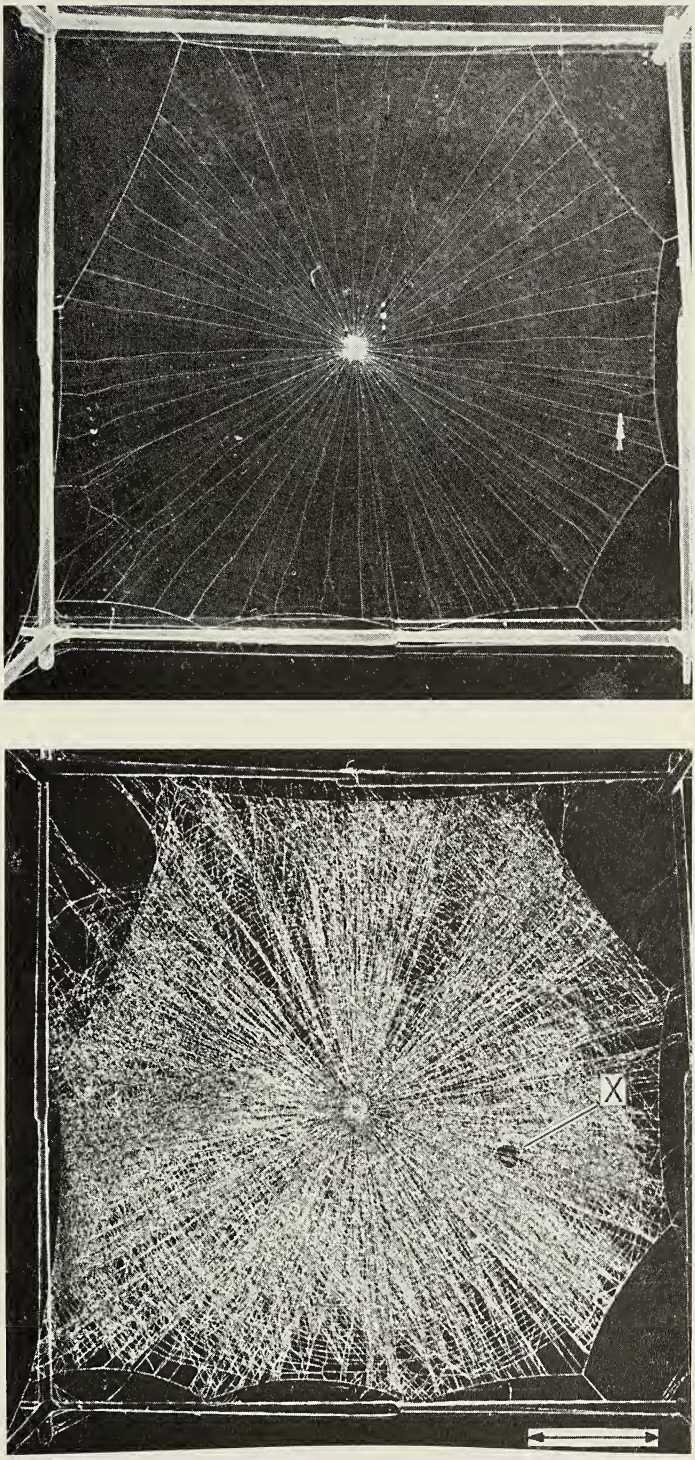

Fig. 1.–Web of second instar *Uloborus diversus*, unpowdered (above) and powdered (below). The spider opened a hole at x to remove prey, then laid several lines across it. Scale marker is 2 cm.

Before the spider left the hub to lay another supplemental radius, it brought both I's close together and tapped or jerked quickly on the threads directly ahead of it. Since the spider invariably laid a radius following these movements, they do not appear to function as do similar movements made during ordinary radius construction to sense cues used in deciding whether or not to construct a radius in the sector in front of the spider; their function is not clear. The spider moved from the hub toward the frame along a previously laid radius, but often stopped before it reached the frame and attached the new supplementary radius to this radius. After moving between one-third and one-half the way back toward the hub (apparently under the line or lines just laid), the spider tapped its abdomen against the web (probably attaching the line(s) it was laying to the web), broke the line(s) legs I were holding, and let out silk. The spider, which now formed a bridge between the line(s) running from its legs I to the hub and the line(s) running from its spinnerets to the attachment it had just made, descended several millimeters as it let out silk, then gradually reascended as it moved toward the hub, apparently reeling in the line in front of it and laying a new one(s) behind.

Non-radial lines were somehow produced during construction of additional radii, but it proved impossible to see them without powdering the web, and this effectively stopped construction behavior. Each additional radius construction trip resulted in the placement of several lines, and when webs were powdered just after construction of supplemental radii had begun, there were several lines in each sector in which the spider had made a trip. The non-radial lines may have been produced when the spider broke some of these lines in subsequent trips and the broken ends drifted in the air before sticking somehow to the web. Loose lines must have played some part in the process, since the spiders never moved in non-radial directions, and since, although the spider never moved past the frame threads, there were often lines beyond the frames in finished webs. The construction of supplementary radii was not a continuous process, and long periods of inactivity (up to an hour or more) occurred between bursts of construction.

All webs of second instar *U. diversus* had accumulations of white silk at the hub similar to those observed by Wiehle (1927). These accumulations were absent from webs not containing supplementary radii, and became more and more prominent during the course of supplementary radius construction. They may be the lines the spiders broke and rolled up (?) as they returned to the hub during supplemental radius construction.

Second instar *U. diversus* did not make the stabilimenta characteristic of the species (Eberhard, 1974). They stayed at the hubs of their webs most of the time, and were less likely to run to the edge in response to disturbing stimuli than were older spiders.

Szlep (1961) emphasized that the pause which occurred between termination of temporary spiral construction was analogous to a pause between temporary spiral and sticky spiral construction in later instars. Second instar *U. diversus* did not pause after termination of temporary spiral construction, however, while adult spiders paused for periods varying from less than five seconds to about a minute. The length of these pauses does not seem to be of particular importance in understanding the evolution of web patterns or the cues directing web construction.

Third instar *U. diversus* also constructed intermediate-type webs similar to those of *U. plumipes* and *U. walckenaerius* described by Szlep (1961) which contained supplementary radii and temporary spirals as well as sticky spirals. These webs, which also had mats of non-radial lines, were sometimes spun by third instar nymphs which had already constructed adult-type orbs. Some of the additional radii may have been added on nights after the web was first built, as construction of supplementary radii by a third instar

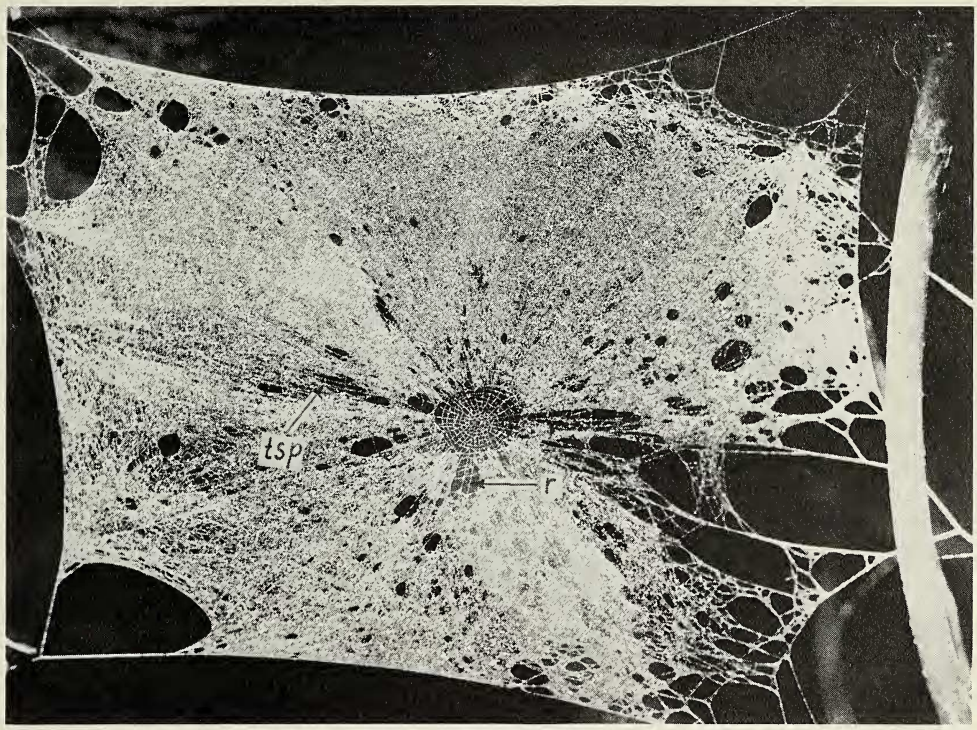

Fig. 2.–Web of mature male *Uloborus* sp.; r is a radius, tsp a temporary spiral, and the arrow marks a mat of fine threads. The more or less oval holes were probably caused by raindrops. Scale marker is 3 cm.

spider was seen once on the night following original web construction. The factor(s) responsible for the production of intermediate-type rather than adult-type webs by post-second instar spiders are not known.

Fig. 2 shows the web on which a mature male *Uloborus* sp. (specimen No. 1015) was found resting at the hub at about 9 A.M. in the understory of secondary tropical forest on Barro Colorado Island in the Panama Canal Zone. It was almost certainly made by the male as there were no other webs or spiders nearby. Two other similar webs with males at their hubs were found in the early evening (specimens Nos. 879 and 890), and another (No. 902), which shared the frame threads of the orb of a mature female, was found in the late morning on the mainland near the canal. All four webs were perfectly, or nearly perfectly, planar, and more nearly horizontal than vertical. The two night webs showed no obvious damage, and appeared to be newly built, while the day web not illustrated was somewhat tattered.

The web in Fig. 2 clearly has the same elements–radii (r), temporary spiral (tsp), and dense mats of very fine radial and non-radial threads–as second instar spiderlings' webs.

DISCUSSION

It appears that the construction of orb webs with sheets of very fine silk rather than sticky spirals may be widespread or universal among second instar *Uloborus* spiderlings. In addition to the five species now reported on, I have seen such webs in *U. arizonicus*, and both Y. D. Lubin (pers. comm.) and I have seen them in a number of other, as yet unidentified, tropical species. The adaptive significance of this web design is unclear, and

it is not certain which came first—the lack of a functional cribellum in the second instars, or the second instar web. Construction of this type of web involves only one behavioral sequence not seen in typical orb construction, and does not seem to be a particularly large evolutionary step. The fact that an older spider with a functional cribellum may sometimes produce a second instar-type web cannot be interpreted without testing the possibility that internal states (such as dehydration) selectively influence the production of cribellum silk. The similarity between second instar *Uloborus* webs and those of "senile" virgin female *U. diversus* is striking (Eberhard, 1971).

The resemblance of the mature male *Uloborus* sp. webs to those of second instar nymphs is almost certainly due to the fact that mature males also lack a functional cribellum. Within the genus this reduction is associated with the general lack of webs made by mature males, and the webs of these Panamanian *Uloborus* sp. should thus not be considered a relict of former times when males spun webs, but a reacquisition of immature behavior, possibly to increase the life span of the mature males.

Apparently the only published record of a mature male orb weaver with his own orb is that of Robinson and Robinson (1973) for *Nephila maculata* (Araneidae); these males may not have been mature, however (M. Robinson, pers. comm.). I have however seen mature males of *Mecynogea* (?) with small sheet webs within the meshes above the females' sheet webs, a mature male of a colonial species of *Cyclosa* on his own orb, and mature males of several species of Symphytognathidae with their own orbs.

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